

Pacific Mexican Affinities of New Species of the Gastropod Genera *Macron* (Pseudolividae) and *Neorapana* (Muricidae) from the Cantaure Formation (Early Miocene) of Venezuela

by

JACK GIBSON-SMITH AND WINIFRED GIBSON-SMITH

6N Oak Lodge, Lythe Hill Park, Haslemere, Surrey GU27 3TF England

AND

GEERAT J. VERMEIJ¹

Department of Geology and Center for Population Biology, University of California at Davis,
Davis, California 95616 USA

Abstract. *Macron constrictus* sp. nov. and *Neorapana rotundata* sp. nov. from the Cantaure Formation (Early Miocene) of Venezuela are the earliest known members of their respective genera, and the only species of *Macron* and *Neorapana* known from the Atlantic Ocean. Both are extremely similar to Recent species from northwestern Mexico, *Macron orcutti* Dall, 1918, and *Neorapana tuberculata* (Sowerby, 1835).

INTRODUCTION

The very rich early Miocene fauna of the Cantaure Formation of Venezuela contains representatives of many genera that are rarely preserved as fossils. Here we describe two new species, *Macron constrictus* (Pseudolividae) and *Neorapana rotundata* (Muricidae). Not only are these species the earliest known members of their respective genera, but they also provide evidence of geographical restriction of *Macron* and *Neorapana* to the eastern Pacific, notably to northwestern Mexico. The two species are characterized by a labral tooth, a common feature among Cantaure neogastropods. Abbreviations used in the text: LACM, Los Angeles County Museum of Natural History; NMB, Naturhistorisches Museum, Basel; UCMP, University of California, Museum of Pa-

leontology, Berkeley; USNM, United States National Museum of Natural History.

SYSTEMATICS

Family PSEUDOLIVIDAE Cossmann, 1901

Genus *Macron* H. & A. Adams, 1853

Type species: *Macron aethiops* (Reeve, 1847).

Macron constrictus J. Gibson-Smith &
W. Gibson-Smith & Vermeij, sp. nov.
(Figures 1–3)

Macron orcutti Dall: Gibson-Smith & Gibson-Smith, 1979:22.

Diagnosis: *Macron* with very finely threaded, rounded last whorl, narrowly channeled suture in adult stage, and inner side of outer lip bearing 13 to 16 lirae on recessed ridge.

¹ To whom correspondence should be addressed.



Figures 1–3

Ventral, dorsal, and oblique apical views of *Macron constrictus* J. Gibson-Smith & W. Gibson-Smith & Vermeij, sp. nov.; holotype, NMB 17776; 36.7 mm in height.

Description: Shell medium-sized, maximum height 36.6 mm, fusiform; spire relatively high, last whorl comprising 68–72% of total shell height; protoconch consisting of two and one-half to three smooth, bulbous whorls; junction between protoconch and teleoconch indistinct; teleoconch consisting of four to five whorls separated by distinct suture, which becomes narrowly channeled between penultimate and last whorl of adult specimens; last whorl without shoulder, evenly rounded on upper part, weakly constricted near base; area immediately below suture on last two whorls weakly concave; spiral sculpture of first teleoconch whorl consisting of five cords; spiral sculpture of first teleoconch whorl consisting of five cords; spiral sculpture of later whorls consisting of very fine striae, which continue to the upper part of the last whorl; lower part of last whorl with deep spiral groove (pseudolivid groove), below which are two or three flat, low spiral cords; axial sculpture absent; outer lip planar, its edge crenulated most strongly by the ends of interspaces between basal cords; labral tooth present, consisting of a blunt projection at the edge of the outer lip, situated at the end of a deep spiral groove (pseudolivid groove); inner side of outer lip thickened by ridge parallel to edge, sculptured by 13 to 16 short lirae; adapical end of outer lip with weak notch; inner lip adherent, smooth, with broad, rounded fold at entrance of siphonal canal; adapical end of inner lip bearing rounded parietal rib; colu-

mellar and parietal callus of very limited extent; aperture ovate, its height-to-breadth ratio 2.4 to 2.6; siphonal fasciole prominent, bounded adapically by low keel; umbilicus absent.

Holotype: NMB Number 17776; height 36.7 mm, diameter 21.5 mm, height of aperture 26.5 mm.

Paratypes: 18 specimens. Paratype 1: NMB H-17777, height 36.2 mm, diameter 22.6 mm. Paratype 2: NMB H-17778, height 34.2 mm, diameter 20.3 mm. Paratype 3: NMB H-17779, height 29.2 mm, diameter 17.8 mm. Paratype 4: NMB H-17780, height 30.5 mm, diameter 18.1 mm. Paratype 5: NMB H-17781, height 10.9 mm, diameter 6.5 mm. UCMP 152334, three specimens, largest height 35.5 mm, diameter 22.3 mm, height of aperture 24.2 mm.

Type locality: GS-1-PGNA, NMB 17516, lower shell bed, Cantaure Formation, 300 m south southeast of the new (1952) Casa Cantaure near San José de Cocodite, Paraguaná Peninsula, Falcón State, Venezuela.

Stratigraphic and geographic distribution: Cantaure Formation (Early Miocene), Venezuela.

Discussion: In reviewing the fauna of the Cantaure Formation of Venezuela, Gibson-Smith & Gibson-Smith (1979:22) listed *Macron orcutti* Dall, 1918, and recog-

nized this species as Paciphilic, that is, as having become restricted to the eastern Pacific from a broader distribution that also included the Atlantic. This fossil is indeed strikingly similar to *M. orcutti*, which occurs in the Recent fauna from Bahía Magdalena south to Punta Marquez, on the Pacific side of Baja California Sur, Mexico. Because the fossil form differs significantly and consistently from the Recent *M. orcutti*, we here distinguish it as a separate species, *M. constrictus*. The material of *M. orcutti* on which the comparisons below are based consists of the holotype (USNM 218185) from Magdalena Bay, and two additional lots, LACM 79-26.27 (Punta Marquez) and LACM 71-3.26 (Punta Abreojos). The latter two lots were kindly loaned to GJV by J. H. McLean.

The Miocene *Macron constrictus* from the Cantaure Formation resembles the Recent *M. orcutti* in maximum adult size (36 mm in both species), spire height (last whorl comprising 68–72% of shell height in *M. constrictus*, 60–75% in *M. orcutti*), aperture shape (height-to-breadth ratio 2.4–2.6 in both species), number of lirae on the inner side of the outer lip (13–16 in *M. constrictus*, 13–17 in *M. orcutti*), and in having the last whorl evenly rounded and mostly smooth, with spiral sculpture being confined to the basal part. *M. constrictus* differs from *M. orcutti* by having the suture narrowly channeled instead of appressed between the last two whorls, by being somewhat more constricted basally, by having a concave zone just below the suture, and by having the inner side of the outer lip thickened.

With the recognition of *M. constrictus*, the genus *Macron* must be added to the list of Paciphilic taxa. *M. constrictus* is only the second pseudolivid known from the Neogene in the western Atlantic. The only other Neogene member of the family there is *Pseudoliva guppyi* Mansfield, 1925, from the Miocene of Trinidad.

All the available specimens are from the lower shell bed of the Cantaure Formation. Stratigraphic relations and the fauna of planktonic Foraminifera indicate that the Cantaure Formation is of Early Miocene (Burdigalian) age (Díaz de Gamero, 1974; Gibson-Smith & Gibson-Smith, 1979; González de Juana et al., 1980).

The holotype and two paratypes each have one repaired break on the last whorl. The incidence of shell repair among the 22 available specimens is therefore 14%.

Family MURICIDAE Rafinesque, 1815

Subfamily RAPANINAE Gray, 1853

Genus *Neorapana* Cooke, 1918

Type species: *N. muricata* (Broderip, 1832).

Neorapana rotundata J. Gibson-Smith & W. Gibson-Smith & Vermeij, sp. nov.

(Figures 4–9)

Diagnosis: *Neorapana* with the periphery below the shoulder at the third of five primary spiral cords on last whorl.

Description: Shell of medium size, maximum height estimated to be 38 mm, broadly fusiform; protoconch not preserved; teleoconch consisting of about four whorls separated by impressed suture; spire relatively high, last whorl comprising 69–79% of total shell height; last whorl with low, angulated shoulder above, tapering without constriction below; last whorl sculptured by five primary spiral cords, each bearing eight tubercles in the adult and 15 in the immature shell; second primary cord from suture forms shoulder; third primary cord forms periphery of last whorl; aperture ovate, its height-to-breadth ratio 2.2 to 2.5; outer lip incompletely preserved, but shows a trace of a labral tooth at end of groove below fifth primary cord; inner side of outer lip smooth or with six weak denticles; columella straight, smooth, its upper end marked by parietal rib; inner lip adherent along most of its length, but forming excavated, free-edged flange below prominent siphonal fasciole; umbilicus absent.

Holotype: NMB H-17784; height 35.6 mm, maximum diameter 28.22 mm, height of aperture 24.5 mm.

Paratypes: Paratype 1: NMB H-17783; height 33.3 mm, maximum diameter 30.6 mm (incomplete). Paratype 2: NMB 17782; height 17.7 mm, maximum diameter 13.7 mm.

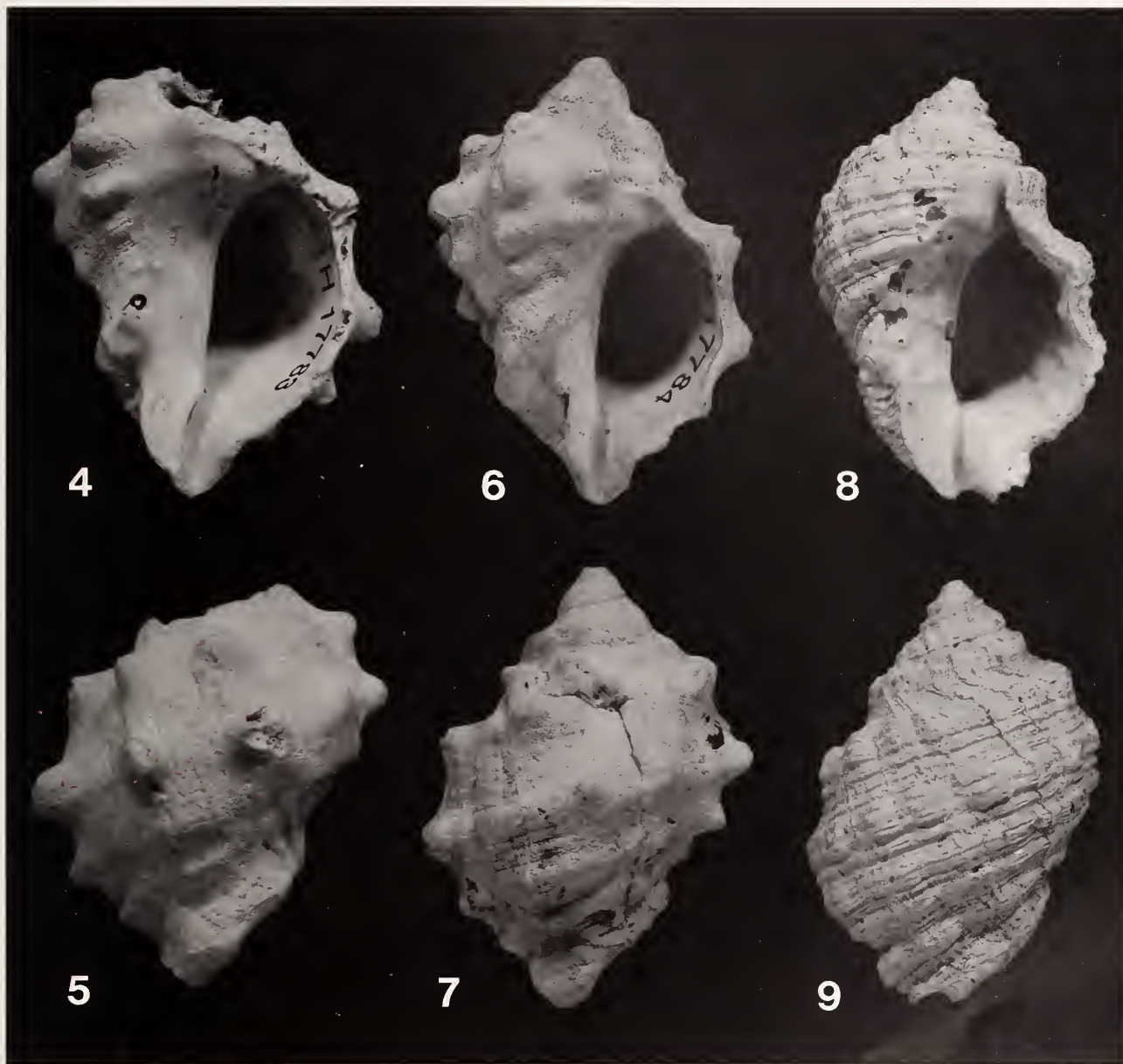
Type locality: GS-122-PGNA, NMB 17519, upper shell bed, Cantaure Formation, 550 m southeast of the new (1952) Casa Cantaure near San José de Cocodite, Paraguaná Peninsula, Falcón State, Venezuela.

Stratigraphic and geographic distribution: Cantaure Formation (Early Miocene, Burdigalian), Venezuela.

Etymology: *rotundata*, Latin “rounded,” referring to the profile of the upper part of the last whorl.

Discussion: The above description is based on three specimens, none of which is wholly intact. In the holotype, collected by J. and W. Gibson-Smith at their Locality GS-122-PGNA from the upper shell bed in the Cantaure Formation, the excavated anterior portion of the inner lip is abraded. Paratype 1, also from the upper shell bed, has the spire missing, and with a maximum shell diameter of 30.6 mm, is the largest of the three specimens, with an estimated height of 38 mm. The labral tooth is preserved only on Paratype 2, an immature shell from Locality GS-1-PGNA in the lower shell bed of the Cantaure formation.

We assign this species to the genus *Neorapana* on the basis of the following characters: five tuberculated primary spiral cords; presence of labral tooth at end of groove below fifth primary cord; lower part of inner lip free-edged and slightly excavated; broadly ovate aperture; smooth, straight columella; parietal rib present. The only character inconsistent with assignment to *Neorapana* is the smooth inner side of the outer lip in the two apparently mature specimens (the holotype and



Figures 4, 5

Ventral and dorsal views of *Neorapana rotundata* Gibson-Smith & Vermeij, sp. nov.; paratype 1, NMB H-17783; height 33.3 mm.

Figures 6, 7

Ventral and dorsal views of *Neorapana rotundata* J. Gibson-Smith & W. Gibson-Smith & Vermeij, sp. nov.; holotype, NMB H-17784; height 35.6 mm.

Figures 8, 9

Ventral and dorsal views of *Neorapana rotundata* J. Gibson-Smith & W. Gibson-Smith & Vermeij, sp. nov.; paratype 2, NMB H-17782; height 17.7 mm.

paratype 1). In the immature paratype 2, the inner side of the outer lip bears six weak denticles or riblets. The three Recent species of *Neorapana* are characterized by a lirate outer lip, in which discontinuous riblets occur

on the inner side. In two immature specimens of *N. tuberculata* (Sowerby, 1835) in the Vermeij collection from Estero de Bahía Falso (southern Gulf of California, Baja California Sur), however, the inner side of the

outer lip is smooth as it is in the two larger *N. rotundata* from Venezuela.

The fossil *N. rotundata* very closely resembles the Recent northwest Mexican *N. tuberculata* (Sowerby, 1835). *N. rotundata* differs from *N. tuberculata* mainly in having the widest part of the shell at cord three, below the shoulder; whereas in *N. tuberculata* the widest part of the shell encompasses the sector bounded by the second and third primary cords. *N. rotundata* therefore gives a more rounded aspect than does *N. tuberculata*.

In a phylogenetic analysis of the subfamily Rapaninae, Vermeij & Carlson (in review) identified the Indo-West Pacific genus *Mancinella* Link, 1807, as the sister group of *Neorapana*. The Miocene *N. rotundata* resembles species of *Mancinella* more closely than do any of the three Recent species of *Neorapana*. Both *N. rotundata* and species of *Mancinella* have the widest part of the shell at the third primary spiral cord of the last whorl, below the shoulder; whereas in the living *Neorapana*, the widest part is either at the shoulder (the second primary cord), as in *N. muricata* and *N. grandis* (Sowerby, 1835), or in the sector bounded by the second and third primary cords, as in *N. tuberculata*.

As pointed out by Vermeij & Kool (1994) and Vermeij & Carlson (in review), the labral tooth of *Neorapana* evolved independently of that in *Mancinella*. In *Neorapana*, the labral tooth is formed at the end of a groove situated below the fifth primary cord. In *Mancinella alouina* (Röding, 1798), the type species of *Mancinella*, it forms at the end of a groove between the fourth and fifth primary cords. Other Indo-West-Pacific species of *Mancinella* lack a labral tooth (see Vermeij & Carlson, in review, for a review of species of *Mancinella* and *Neorapana*). The discovery of *N. rotundata* shows that the evolution of the labral tooth in *Neorapana* had already occurred by Early Miocene time.

Neorapana rotundata is phylogenetically interesting for three additional reasons. First, it is the earliest known member of its genus. Previously, the genus had been recorded from the Pliocene of the Gulf of California (as *Acanthina* cf. *A. tuberculata* Sowerby by Durham, 1950, and Emerson & Hertlein, 1964) and from the La Vaca Formation (Pliocene) of Costa Rica (as *Neorapana* sp. in a list by Woodring, 1973). Second, *N. rotundata* is the only species of its genus from the Atlantic side of tropical America. The genus *Neorapana* must therefore be added to the list of clades that have become restricted since Late Neogene time to the eastern Pacific. Third, like *Macron constrictus*, *N. rotundatus* has as its closest apparent relative a Recent species from northwestern Mexico. The two other Recent species of *Neorapana*, *N. muricata* from the mainland coasts of Central and northwestern South America, and *N. grandis* from the Islas Galápagos, differ from *N. tuberculata* and *N. rotundata* in being much larger and in having a markedly triangular last whorl whose widest point coincides with the sharply angular shoulder.

DISCUSSION

The molluscan fauna of the Cantaure Formation is remarkable not only for its richness, with more than 600 species being recorded (see Jung, 1965, and Gibson-Smith & Gibson-Smith, 1979, for a partial account), but also because it records the earliest appearance of many genera in tropical America, including *Macron* and *Neorapana*. Many taxa in the Cantaure Formation, moreover, belong to Paciphilic clades. At least one taxon in the Cantaure Formation other than *Macron* and *Neorapana* has as its closest living relative a species in northwestern Mexico. The turrid *Glyphostoma* (*Euglyphostoma*) is represented today by a species in the Gulf of California.

Both *Macron* and *Neorapana* possess a labral tooth on the edge of the outer lip. Other species in the Cantaure formation with a labral tooth include *Panamurex gatuensis* (Brown & Pilsbry, 1911) (see Vokes, 1992) and new species of *Ocinebrina* and *Pterorytis* (*Microrhytis*) (see Vermeij & Vokes, 1997). A labral tooth therefore occurs in four of at least 20 muricids (20%) in the Cantaure Formation. This is the highest incidence of labral teeth in any muricid assemblage in tropical America, fossil or Recent. Work in progress by Vermeij indicates that this high incidence is typical of communities living under condition of high planktonic productivity.

ACKNOWLEDGMENTS

We thank Mary Graziose for photographs, Janice Cooper for technical assistance, and NSF Grant EAR-94-05537 to Vermeij for partially funding this research.

LITERATURE CITED

- ADDICOTT, W. O. 1970. Miocene gastropods and biostratigraphy of the Kern River area, California. U.S. Geological Survey Professional Paper 642:1-174.
- DÍAZ DE GAMERO, M. L. 1974. Microfauna y edad de la Formación Cantaure, Península de Paraguaná, Venezuela. Boletín Informativo de la Asociación Venezolano de Geología, Mineralogía, y Petrología 17:41-47.
- DURHAM, J. W. 1950. 1940 E. W. Scripps Cruise to the Gulf of California II. Megascopic paleontology and marine stratigraphy. Geological Society of America Memoir 43:1-216.
- EMERSON, W. K. & L. G. HERTLEIN. 1964. Invertebrate megafossils of the Belvedere Expedition to the Gulf of California. Transactions of the San Diego Society of Natural History 13:333-368.
- GIBSON-SMITH, J. & W. GIBSON-SMITH. 1979. The genus *Arcinella* (Mollusca: Bivalvia) in Venezuela and some associated faunas. GEOS 24:11-32 [Escuela de Geología y Minas, Universidad Central de Venezuela, Caracas].
- GONZÁLEZ DE JUANA, C., J. M. ITURRALDE DE AROZENA & J. PICCARD CADILLAT. 1980. Geología de Venezuela y de sus cuencas petrolíferas, Tomo 2. Ediciones Foninves, Caracas, pp. 415-1031.
- JUNG, P. 1965. Miocene Mollusca from the Paraguaná Peninsula, Venezuela. Bulletins of American Paleontology 49:389-652.
- VERMEIJ, G. J. & S. P. KOOL. 1994. Evolution of labral spines

- in *Acanthais*, new genus, and other rapanine muricid gastropods. *The Veliger* 37:414–424.
- VERMEIJ, G. J. & E. H. VOKES. 1997. Cenozoic Muricidae of the western Atlantic region. Part XII—The subfamily Ocenebrinae (in part). *Tulane Studies in Geology and Paleontology* 29:69–118.
- VOKES, E. H. 1992. Cenozoic Muricidae of the western Atlantic region. Part IX - *Pterynotus*, *Poirieria*, *Aspella*, *Dermomurex*, *Calotrophon*, *Acantholabia*, and *Attiliosa*; additions and corrections. *Tulane Studies in Geology and Paleontology* 25: 1–108.
- WOODRING, W. P. 1973. Affinities of Miocene molluscan families on Pacific side of Central America. *Publicaciones Geologicas del Instituto Centroamericano de Investigaciones Tecnologicas y Industriales* 4:179–188.